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Drought-tolerance of an invasive alien tree, *Acacia mearnsii* and two native competitors in fynbos riparian ecotones

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Abstract Invasive alien plants (IAPs) have successfully invaded many riparian zones in South Africa, especially Australian *Acacia* spp. which are prevalent along riverbanks in the south-western Cape of South Africa. This Mediterranean-type climate region is predicted to endure severe future water shortages under likely scenarios of increased population growth and climate change, and IAPs aggravate this problem due to their profligate water use. *Acacia mearnsii* competes aggressively with native species, however, it remains unclear what physiological advantage the species has over co-occurring native species under the predicted reduced streamflow scenarios. A mechanistic approach was used to investigate how key native fynbos riparian woody tree species compare in vulnerability to drought-induced cavitation against *A. mearnsii* by comparing findings from three Mediterranean-type fynbos river systems that differ in streamflow. *A. mearnsii* showed lower water potential at 50% hydraulic conductivity loss (P_{50} values) compared to native species at certain sites, an indication of drought-tolerance. This suggests it is likely to persist under future drier conditions and it therefore remains a top priority for control. The native *Brabejum stellatifolium* had consistently higher water potentials across all sites than the other studied species, and is a potentially valuable species for restoration of south-western Cape riparian zones. Consistency in the shapes of species vulnerability curves across sites illustrated a species-specific hydraulic response to different water availability, strengthening the argument that this approach to distinguish site-level drought-tolerance between trees is a practical technique, with great application in understanding future geographic distribution under climate change, and potential for use in restoration research. Additionally, streamflow was an inaccurate predictor of species drought-tolerance along these riparian systems.

Keywords Invasive alien plant · Water potential · Carbon isotope · Restoration · Streamflow · Xylem cavitation

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Introduction

Freshwater in South Africa is widely recognised as a dwindling resource that will severely inhibit future socio-economic growth (Davies and Day 1998; Walmsley et al. 1999). Global climate change could aggravate the already limited water situation (Schulze

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et al. 2001; Meadows 2006) and endanger plant and animal species associated with rivers and riparian wetlands. Climate change predictions indicate that Mediterranean-type ecosystem rivers in the south-western Cape face declining runoff (Steynor et al. 2009) and may lose between 14 and 32% of their total streamflow due to a combination of declining runoff and water extraction from urban areas (New 2002). These hydrological systems are therefore highly vulnerable and there is justifiable concern for the ecological stability of river systems and the subsequent matters pertaining to water resource management. Invasions by woody alien plant species aggravate this problem due to the propensity of these plants to use large amounts of water.

Invasive alien plants (IAPs) are a global concern as they have an enormous impact on biodiversity, water resources and ecosystem services. The loss in water resources associated with high evapotranspiration rates from IAPs in South Africa has especially caused concern. The effects that invasive alien timber plantations and escapees from plantations have on water resources, particularly streamflow quantities has received much attention (Bosch and Hewlett 1982; Le Maitre et al. 1996, 2002; Scott et al. 1998; Dye and Jarmain 2004). Results vary but generally show a significant reduction in streamflow quantity in catchments planted to exotic plantations and in riparian zones converted to stands of IAPs. Additionally, some *Acacia* species have been shown to exhibit high resistance to drought-induced xylem cavitation (Maherali et al. 2004), and thus, should they be introduced outside their native ranges, they have the potential to outcompete native species and persist under drier conditions predicted for many parts of South Africa. It is not known whether this apparent advantage holds for woody IAPs in South Africa, and more specifically for *Acacia mearnsii* in the south-western Cape. This is in addition to a suite of other advantages *Acacia* species have e.g. increased photosynthetic capacity (Kraaij and Cramer 1999; as reviewed in Morris et al. 2011). Investigating whether *A. mearnsii* is more drought tolerant than native species and whether this holds for rivers of different sizes can aid strategic planning and expenditure and ultimately more effective conservation management and ecosystem restoration, necessary after clearing of invasions takes place (Richardson and Van Wilgen 2004). As an example, this information would enable us to predict and prioritize areas where the IAP holds the physiological advantage. A recent study showing differences in vulnerability of native fynbos riparian vegetation has shown the value of this type of research (Swift et al. 2008).

In order to understand the physiological basis for plant adaptations to drought, Sperry et al. (1988) developed a technique that measures the level of xylem cavitation in plant stems. This method essentially relates xylem water potentials to loss in xylem hydraulic conductivity due to chronic water deficit when excised stems are allowed to dehydrate (Tyree and Sperry 1988). The end result is a vulnerability curve, which is useful to evaluate different species' vulnerability to cavitation by comparing xylem water potential against the point where 50% hydraulic conductivity is lost (50% of xylem cavitated), referred to as the P_{50} value (e.g. Hacke et al. 2000; Wheeler et al. 2005; Maherali et al. 2006; Swift et al. 2008). The study of vulnerability to cavitation has been applied to many different ecological questions, e.g. determining the variation in drought-tolerance between subspecies (Kolb and Sperry 1999); determining the underlying mechanism of tree distribution (Pockman and Sperry 2000); variance in drought resistance between important agricultural cultivars (Wikberg and Ögren 2004; Cochard et al. 2008); variance in drought resistance between native and alien species (Pratt and Black 2006); and possible impacts of climate change on species survival (Martínez-Vilalta et al. 2002). It has also proved to be an insightful approach in restoration ecology (Swift et al. 2008). Swift et al. (2008) showed how key riparian species in the South African fynbos region had differences in their vulnerability to drought-induced cavitation, with the least vulnerable individuals observed at low streamflow sites. This implies that streamflow may be a valuable proxy for indicating plant water availability although this is not always the correct assumption for riparian species (see e.g. Dawson and Ehleringer 1991). Further exploration of the hypothesis put forward by Swift et al. (2008) that streamflow volume is strongly linked to drought-tolerance, could provide valuable information for restoration managers as a robust tool to predict sites where plants might experience more intense drought-stress.

In addition, drought-tolerance must be seen in conjunction with leaf-level regulation of water as different plants may adopt different ecological

strategies to cope under dry conditions (Lambers et al. 1998). A recent framework by McDowell et al. (2008) emphasized the two main strategies that plants may use to cope with declining water availability. On the one hand, some plants may continue carbon assimilation by keeping stomata open under low water potentials (anisohydry). On the other hand, species close their stomata to prevent excessive loss of water under dry conditions, in so doing relieving cavitation pressure on plants (isohydry). These strategies may manifest in the measured $\delta^{13}C$ values as indicator of water-use efficiency. Seibt et al. (2008) described the potential of $\delta^{13}C$ in understanding possible effects of global warming on WUE, and subsequent species survival strategies. Therefore, at the leaf level, we investigated $\delta^{13}C$ as indicator of water-use efficiency (WUE) where higher $\delta^{13}C$ values indicate higher WUE (Farquhar et al. 1982). It has been suggested that rapid alien invasion, specifically in fynbos, could be attributed to factors such as plant WUE (Kraaij and Cramer 1999; Morris et al. 2011). Therefore understanding if invasive species outcompete native species at the whole plant level (less vulnerable to cavitation) and at the leaf level (better WUE) could prove highly insightful.

Our study addressed the following key questions: (1) In a water-limited scenario, how do key native fynbos riparian woody tree species compare in vulnerability to drought-induced cavitation, xylem water potentials and WUE against the woody tree invasive *A. mearnsii*? (2) Which of the studied key native species will be most suited for restoration? (3) Could streamflow be a robust screening tool when predicting which sites would be most vulnerable to cavitation, as one would expect individuals at high flow sites to be less drought-tolerant, than those in low flow areas (sensu Swift et al. 2008)? We investigated these questions by comparing findings from three Mediterranean-type fynbos river systems that differ in streamflow, ranging from low to high flow.

Methods

Description of species and study sites

The native, predominantly riparian species, *Brabejum stellatifolium* (L.) (Proteaceae) and *Metrosideros angustifolia* (L.) (Myrtaceae) (Coates-Palgrave 2002; Reinecke and King 2007), were selected to study as these evergreen trees, which are the only indigenous species of their genus in South Africa, are key species in south-western Cape Mediterranean-type riparian systems (Prins et al. 2004; Galatowitsch and Richardson 2005). Native species physiology was contrasted with the evergreen invasive woody species *A. mearnsii* DeWild (L.) (Fabaceae), which poses a major threat to functioning of riparian zones in the south-western Cape (Dye and Jarmain 2004). Although *A. mearnsii* can also grow in upland areas under low water availability (for example, it is a forestry tree in some parts of South Africa), it is highly competitive in riparian areas where it characteristically uses large amounts of water (Dye et al. 2001). Research has shown that intra-specific variation in drought-tolerance across wet and dry habitats does exist, where one species that showed high drought-tolerance in the dry areas did not show the same degree of drought-tolerance in wet areas (Mencuccini and Comstock 1997; Sparks and Black 1999). We cannot therefore assume that a species will always outcompete the co-occurring riparian species in terms of drought-tolerance simply because it can also grow in dryland areas (Pratt and Black 2006), as functional convergence in traits has been observed in several ecosystems (Meinzer 2003).

The study sites were the Eerste River at Jonkershoek (33°57.621′S, 18°55.037′E; 200 m a.s.l.), Wit River at Bainskloof (33°34.217′S, 19°08.452′E; 279 m a.s.l.) and Molenaars River at DuToitskloof (33°41.778′S, 19°13.263′E; 297 m a.s.l.), all of which are scrub type riparian zones in the Western Cape of South Africa. Site selection was based on the following criteria: the presence of the selected suite of two native and one invasive species; the river system is invaded and no restoration/clearing has occurred and sites differ in streamflow quantity—i.e. ranging from high to low flow. Jonkershoek (JNK) represents the low flow site, Bainskloof (BSK) the intermediate flow site and DuToitskloof (DTK) the high flow site (Fig. 1).

In Table 1 we summarise the geomorphological characteristics of the rivers. Jonkershoek and Bainskloof are draining catchments with predominantly sandstone geology, while at DuToitskloof, sandstone is mixed with igneous rocks. The Bainskloof site is situated in the Mountain Stream Transitional zone, while the two other sites are in the Upper Foothills, which have a lower gradient. The sampled trees also occupy different elevations above and distances away from the active channel (during low flow conditions).

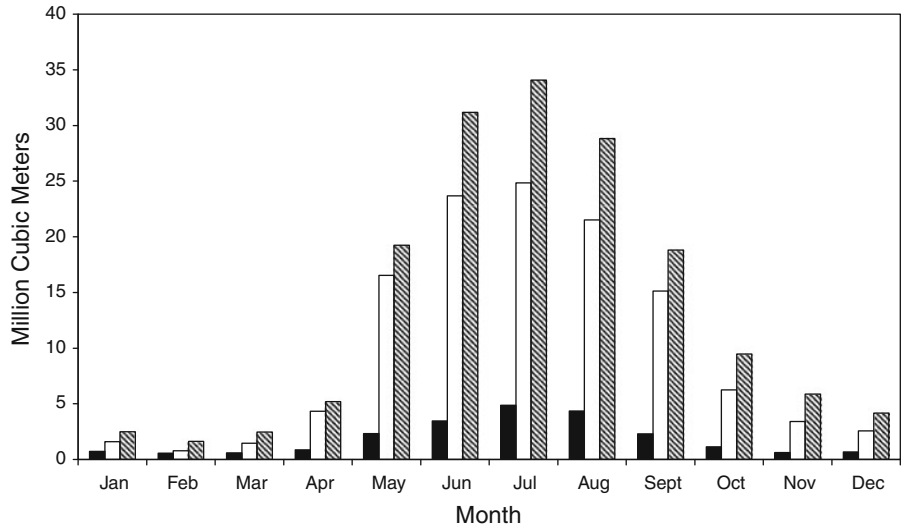

Fig. 1 Mean monthly streamflow at three study sites representing low, intermediate and high streamflow regimes respectively (from 1970 to 2008). Jonkershoek (*black bars*), Bainskloof (*open bars*) and DuToitskloof (*cross-hatched bars*). Data for Jonkershoek were obtained from the CSIR, and that of DuToitskloof and Bainskloof from Department of Water Affairs and Forestry (now Department of Water Affairs)

Table 1 Site-specific information on each of the sites, including the major features of the rivers and the specific river reaches where the sites are situated, as well as pertinent information on the locality of the sample trees in relation to the stream

	Jonkershoek	Bainskloof	DuToitskloof
River	Eerste	Wit	Molenaars
River type (Naiman and Decamps 1997)	Perennial	Perennial	Perennial
Geology	Sandstone	Sandstone	Sandstone and Igneous
Characteristic channel features (according to King and Schael 2001)	Moderately steep, cobble-bed and mixed bedrock-cobble bed channel.	Moderately steep, dominated by bedrock or boulder	Moderately steep, cobble-bed and mixed bedrock-cobble bed channel
Longitudinal Zone (according to King and Schael 2001)	Upper Foothills	Mountain Stream Transitional Zone	Upper Foothills
Range in the distance of sample trees from streams edge during low flow conditions	<2 m	2–10 m	<5 m
Zonation pattern where sample trees were located (Boucher and Tlale 1999; Sieben and Reinecke 2008)	Dry bank	Dry bank	Dry bank
Elevation above stream during low flow conditions	<1 m	1–3 m	<1 m

In addition, visually, the highest cover of alien species (including *Acacia*, *Populus* and *Quercus* spp.) was found at Jonkershoek and at DuToitskloof (predominantly *Acacia*), though a recent fire at the latter site considerably reduced the green biomass. At Bainskloof some clearing occurred on the northern bank, and none on the sampled southern bank (Reinecke and King 2007).

Vulnerability to cavitation

Vulnerability to cavitation was measured using the dehydration method (bench drying method) (Sperry et al. 1988; Pockman and Sperry 2000; Swift et al. 2008). By determining xylem hydraulic conductivity loss due to cavitation, plotted against xylem water potential, drought vulnerability curves were obtained

(Tyree and Sperry 1988). Sampling was conducted during the driest months to capture the period of highest drought stress (lowest water potential) (December 2008–February 2009). Five individuals per species were sampled. Seven branches from each individual were cut at pre-dawn when the first sample was also bagged (to equilibrate transpiration through the plant) for the 0 h measurement. The remaining branches were then transported to the laboratory and allowed to dehydrate for 1, 2, 4, 6, 8 and 10 h on an open laboratory bench. Before measuring stem hydraulic conductivity at each time interval, branches were bagged and left to equilibrate for 1.5–2 h. Ultimately, dehydration of branches should result in the 10 h measurement revealing a 90–100% loss in hydraulic conductivity (xylem 90–100% cavitated). If the required amount of dehydration did not occur, supplementary branches were cut and left for 12–24 h to achieve the desired loss. From each sampled branch, a side branch was cut to measure water potential, using a pressure chamber (Pockman et al. 1995) (PMS instruments, Model 1000, Oregon, USA). The sampled branch was then submerged under water (preventing introduced cavitation) and a stem segment of approximately 10 cm was cut and edges trimmed with a sharp blade. Previous studies on the same species established that xylem vessels did not exceed 10 cm in length (Swift et al. 2008; Swift, pers. comm.). Stems were then connected to the tubing apparatus (as described in Sperry et al. 1988) and initial hydraulic conductivity (K_h) was measured. To obtain maximum conductivity (K_{max}), stems were then flushed for 30 min with 0.1 micrometer filtered, degassed, de-ionised water, at 0.1 MPa (again to prevent introduced cavitation or blockage) and remeasured. Percentage loss in hydraulic conductivity (PLC) for each stem was calculated as:

$$\mathrm{PLC} = 100 \times (1 - K_h/K_{max}) \quad (1)$$

Vulnerability curves for each species were fitted with an exponential sigmoidal equation (Pammenter and Van der Willigen 1998):

$$\mathrm{PLC} = 100/(1 + \exp(a(\Psi - b))), \quad (2)$$

where Ψ is the water potential, PLC is the corresponding loss in hydraulic conductivity and a and b are constants. Water potential where 50% hydraulic conductivity is lost (P_{50}) corresponded to coefficient b in Eq. 2. Significant differences in P_{50}, within and between species and sites, were identified using a test based on the t-distribution, where Bonferroni multiple testing corrections were applied (Statistica Release 8, StatSoft Inc.).

Field xylem water potentials

Stem xylem water potential was measured using a pressure chamber (Pockman et al. 1995) (PMS instruments, Model 1000, Oregon, USA). Measurements were made in summer (December–February), when plants are likely to experience drought stress. Pre-dawn (05h00–05h30) and mid-day (12h00–14h00) measurements were made to obtain maximum (pre-dawn) and minimum (mid-day) water potentials, and were carried out on the same individuals as used for vulnerability curves. Three healthy stems (with leaves) from each individual were cut and measured immediately on site. Three replicates of each treatment were made for each species across all sites. Replicates were conducted on separate days within the month of January 2009. Data were analysed using a factorial ANOVA to determine interactions between sites, species and time of day (pre-dawn or mid-day), followed by a Fisher LSD post-hoc test (Statistica Release 8, StatSoft Inc.).

Foliar carbon isotope analysis

For the $\delta^{13}C$ analyses, ten mature (fresh) leaves from each individual (same individuals as used for vulnerability curves and water potentials) were dried at 40°C until a constant weight was achieved. Leaves were then crushed into a fine powder and analysed for $\delta^{13}C$ by combustion in an automated Elemental Analyzer (Carlo-Erba). The carbon isotope ratio was expressed as:

$$\delta^{13}\mathrm{C}\,(‰) = \left(\left(R_{sample} - R_{standard}\right)/R_{standard}\right) \times 1{,}000 \quad (3)$$

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample, and $R_{standard}$ the PDB standard.

Results

Vulnerability of stem xylem to cavitation

Within species, the slopes of vulnerability curves remained relatively constant across sites (Fig. 2), with

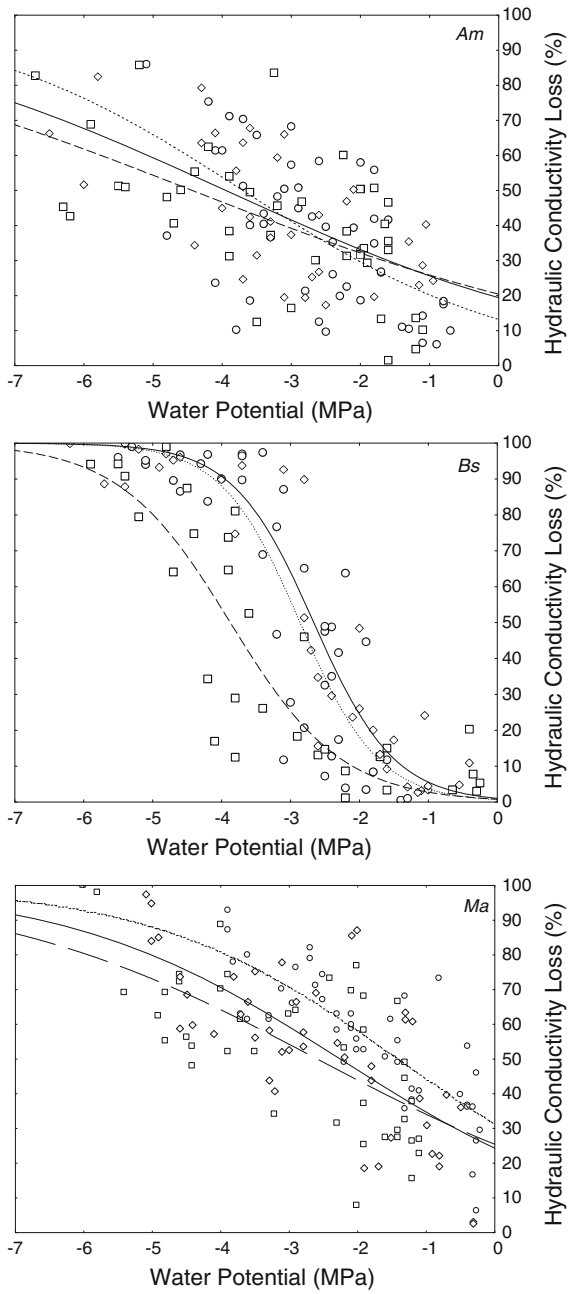

Fig. 2 Vulnerability of stem xylem to cavitation for *Acacia mearnsii* (*Am*), *Brabejum stellatifolium* (*Bs*) and *Metrosideros angustifolia* (*Ma*). *Dotted line* (and *empty circle*) is Jonkershoek, *dashed line* (and *empty square*) is Bainskloof, and the *solid line* (and *empty diamond*) DuToitskloof. *Curves* were fitted by an exponential sigmoidal function (Pammenter and Van der Willigen 1998). Refer to Table 3 for R^2 and P values

only the magnitude of P_{50} values differing (Table 2). At the initiation of measurements *M. angustifolia* and *A. mearnsii* always had a percentage of their xylem already embolised, and then lost conductivity gradually as water potential declined. In contrast *B. stellatifolium* started off with near zero percent of its xylem embolised, but at around −2.5 MPa rapidly started to cavitate. P_{50} values for *B. stellatifolium* were the lowest at Bainskloof (more negative; $P < 0.05$). *M. angustifolia* at Jonkershoek had a significantly higher (less negative) P_{50} than at Bainskloof ($P < 0.05$), but did not differ from DuToitskloof. *M. angustifolia* at Bainskloof and DuToitskloof did not differ significantly from one another. There were no significant differences in P_{50} values for *A. mearnsii* between all sites. *B. stellatifolium* reached 100% loss in conductivity (P_{100}) between −5.5 and −6.5 MPa at Jonkershoek and DuToitskloof, but for Bainskloof P_{100} was achieved at pressures lower than −7 MPa (Fig. 2). Across all sites, neither *M. angustifolia* nor *A. mearnsii* reached P_{100} at pressures higher than −7 MPa (Fig. 2). All species at Bainskloof consistently showed less loss in conductivity at −7 MPa compared to the other two sites. Overall, *A. mearnsii* had the lowest absolute P_{50} values (ranging between −3.70 and −4.43 MPa) and *M. angustifolia* the highest (ranging between −1.42 and −2.59 MPa).

Within individual sites, consistent patterns were evident in the ranking of species' vulnerability to drought-induced cavitation (Fig. 3, Table 2). At Jonkershoek, *M. angustifolia* had a significantly higher P_{50} ($P < 0.05$) than either of the other species. This is the same for Bainskloof. At DuToitskloof however, *A. mearnsii* had a significantly lower P_{50} value ($P < 0.05$) than either of the other species. Overall, species at Bainskloof showed the lowest P_{50} values (ranging between −2.59 and −4.43 MPa), and species at Jonkershoek the highest (ranging between −1.42 and −3.70 MPa).

There was a good relationship (R^2) between water potential and percentage loss in conductivity for both *B. stellatifolium* and *M. angustifolia*, whereas *A. mearnsii* showed consistently relatively weak correlations (Table 3). However, all of the curves were highly significant.

Field xylem water potentials

At Bainskloof, all species showed significantly lower pre-dawn water potentials compared to the two other sites during the measurement period (dry season) ($P < 0.05$; Table 4). Within *B. stellatifolium* and

Table 2 Mean P_{50} values across species and streamflow regime

Site	Streamflow	Species	P_{50}
Jonkershoek	Low	*Brabejum stellatifolium*	-2.86^{bc} (0.09)
		Metrosideros angustifolia	-1.42^{d} (0.14)
		Acacia mearnsii	-3.70^{ab} (0.27)
Bainskloof	Intermediate	*Brabejum stellatifolium*	-3.87^{a} (0.15)
		Metrosideros angustifolia	-2.59^{bc} (0.26)
		Acacia mearnsii	-4.43^{a} (0.43)
DuToitskloof	High	*Brabejum stellatifolium*	-2.66^{c} (0.09)
		Metrosideros angustifolia	-2.26^{cd} (0.22)
		Acacia mearnsii	-3.95^{ab} (0.35)

All values are in MPa. Standard errors are given in parentheses. A test based on the t-distribution was used to compare estimates of the different streamflow treatments. Bonferroni multiple testing corrections were applied. Within and between sites, means with *different superscripts* differ significantly ($P < 0.05$)

M. angustifolia, no significant differences existed in pre-dawn water potentials at either Jonkershoek or DuToitskloof. In contrast, pre-dawn water potentials for *A. mearnsii* at Jonkershoek were significantly higher than at DuToitskloof ($P < 0.05$). Comparisons between species within individual sites revealed that species at Jonkershoek showed no significant difference in their pre-dawn water potential. At DuToitskloof, only *A. mearnsii* had a significantly lower pre-dawn water potential. At Bainskloof all three species differed significantly in their pre-dawn water potentials ($P < 0.05$), with *B. stellatifolium* having the highest water potential (−0.66 MPa), and *A. mearnsii* the lowest (−1.50 MPa).

Within species, across all sites, *B. stellatifolium* showed no significant difference in mid-day water potential (Table 4). *M. angustifolia* at Jonkershoek did not differ significantly from Bainskloof or DuToitskloof, but had a significantly lower water potential at Bainskloof than at DuToitskloof. For *A. mearnsii*, only Bainskloof showed significantly lower mid-day water potentials ($P < 0.05$). Comparisons between species, within and across sites, revealed that *B. stellatifolium* was consistently less water-stressed at mid-day than *M. angustifolia* or *A. mearnsii*, which did not differ from one another.

Foliar $\delta^{13}C$

All species showed their lowest $\delta^{13}C$ at DuToitskloof, the high streamflow site (Table 5). *M. angustifolia* at Jonkershoek and DuToitskloof had a significantly higher $\delta^{13}C$ value ($P < 0.05$) compared to *A. mearnsii* and *B. stellatifolium* at these sites. The latter two species showed no significant difference when compared with each another. At Bainskloof, *B. stellatifolium* and *A. mearnsii* again did not differ significantly, but here, *M. angustifolia* had a significantly higher $\delta^{13}C$ value than *B. stellatifolium*, but not *A. mearnsii*. Overall, *M. angustifolia* showed the highest $\delta^{13}C$ values.

Discussion

It is well known that woody plants display species-specific structural and physiological adaptations to prolonged drought periods (Beikircher and Mayr 2009). In our study, consistency in the shapes of vulnerability curves of the three selected species across all sites (where only the magnitude of measured P_{50} values differed), illustrates that species-specific hydraulic architecture remained relatively intact across sites that differ in water availability. However, the significant changes in magnitude of P_{50} within a species represented in situ adaptation to different degrees of environmental pressure. Swift et al. (2008) found similar differences in P_{50} among different tributaries of the same catchment. Thus, between species, there were diverse responses to hydrological drought (D' Odorico and Porporato 2006), but within species consistent trends were observed. Intra-specific differences between populations confirm that vulnerability to cavitation might either be a plastic response to environment (Pockman and Sperry 2000), or the effect of genetic differences (Kolb and Sperry 1999).

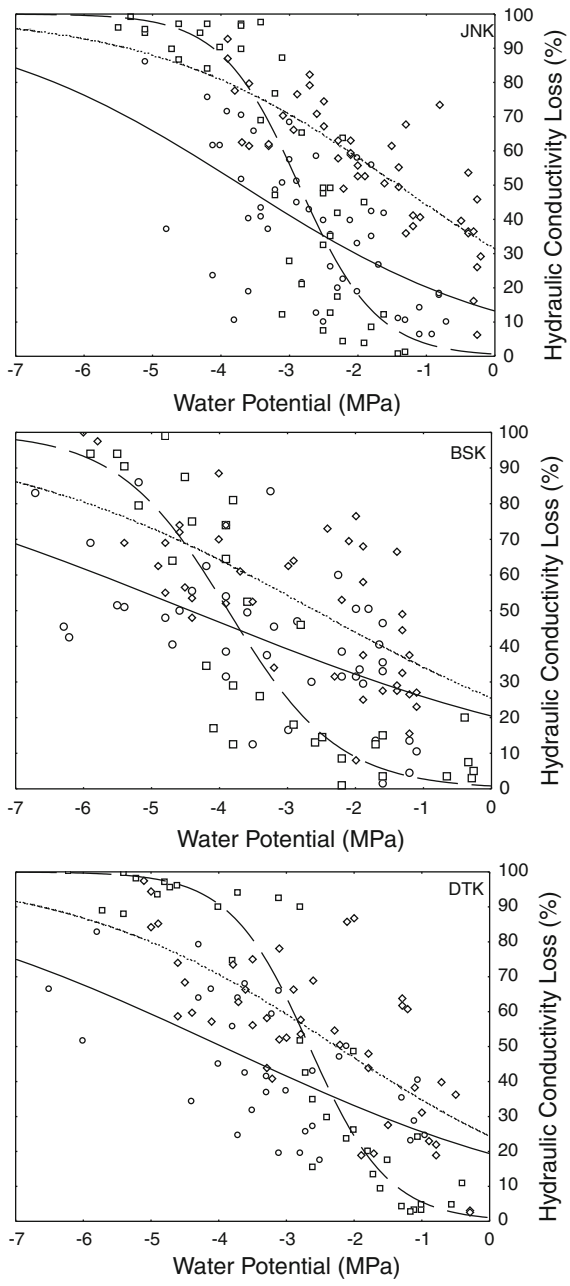

Fig. 3 Vulnerability of stem xylem to cavitation for the studied species at three sites representing low flow, viz Jonkershoek (JNK), intermediate flow, viz Bainskloof (BSK), and high flow, viz DuToitskloof (DTK), streamflow regimes. At each site, the *dotted line* (and *empty diamond*) is *Metrosideros angustifolia*, *dashed line* (and *empty square*) is *Brabejum stellatifolium*, and the *solid line* (and *empty circle*) *Acacia mearnsii*. *Curves* were fitted by an exponential sigmoid function (Pammenter and Van der Willigen 1998). Refer to Table 3 for R^2 and P values

However, more research is needed in this regard (see also Hacke and Sperry 2001).

Of the native species studied, *M. angustifolia* had higher P_{50} values than *B. stellatifolium* at both the low and intermediate flow sites, indicating that the former may be less drought-tolerant (Cochard et al. 2008). However, at the high flow site there was no clear difference in vulnerability to cavitation between the native species. In general, the invasive alien *A. mearnsii* showed evidence of being more drought-tolerant across all sites. However, only at DuToitskloof did it show significantly greater drought-tolerance than both native species, as *B. stellatifolium* did not differ significantly from the invasive species at the other sites. In contrast, *A. mearnsii* always showed higher drought-tolerance than *M. angustifolia* within each site. These results indicate that for the selected native species, *B. stellatifolium* is the most drought-tolerant and thus better adapted to drier conditions than *M. angustifolia*. This confirms findings of Swift et al. (2008), who worked on the Eerste River and adjacent river catchments. The threat of persistence of *A. mearnsii* as an invader in drought prone Mediterranean climates (dry summers) becomes apparent as it clearly exhibited lower P_{50} values at certain sites and in contrast to some native species. Field xylem water potentials further support the contention that the invasive *A. mearnsii* has a significant advantage over some native species under drier conditions.

Minimum field water potential (Ψ_{min}) is an important measure of plant water status, as it represents the minimum moisture status plants must tolerate to remain physiologically active (Bhaskar and Ackerly 2006). Our results indicated, as with vulnerability to cavitation, that within and between species and sites there were significant differences in water potentials at pre-dawn and mid-day. For Mediterranean-type ecosystems, Bhaskar et al. (2007) found an evolutionary link between minimum water potentials (mid-day) and xylem structure, with plants experiencing low water potentials having more drought-tolerant xylem. However, our data revealed that the least drought-tolerant species, *M. angustifolia* shared the same water potential in response to water-stress conditions as the very drought-tolerant *A. mearnsii* which had a greater safety margin against water potentials that would cause 50% of its xylem to cavitate (P_{50}) and so induce runaway cavitation. So, even though *A. mearnsii* had low pre-dawn and mid-day water potentials, it

Table 3 R^2 values and probability (P) of fitted vulnerability to cavitation curves for species across all sites

Site	Species	Equation	R^2	P
Jonkershoek	*Brabejum stellatifolium*	$y = 100/(1 + \exp((1.75375)*(x-(-2.8606))))$	0.76	<0.001
	Metrosideros angustifolia	$y = 100/(1 + \exp((.555544)*(x-(-1.4174))))$	0.65	<0.001
	Acacia mearnsii	$y = 100/(1 + \exp((.508276)*(x-(-3.7012))))$	0.38	<0.001
Bainskloof	*Brabejum stellatifolium*	$y = 100/(1 + \exp((1.23879)*(x-(-3.8726))))$	0.76	<0.001
	Metrosideros angustifolia	$y = 100/(1 + \exp((.414685)*(x-(-2.5904))))$	0.46	<0.001
	Acacia mearnsii	$y = 100/(1 + \exp((.306903)*(x-(-4.4311))))$	0.35	<0.001
DuToitskloof	*Brabejum stellatifolium*	$y = 100/(1 + \exp((1.7069)*(x-(-2.6617))))$	0.90	<0.001
	Metrosideros angustifolia	$y = 100/(1 + \exp((.50287)*(x-(-2.256))))$	0.53	<0.001
	Acacia mearnsii	$y = 100/(1 + \exp((.360492)*(x-(-3.9484))))$	0.38	<0.001

Table 4 Mean values for summer Pre-Dawn (Ψ_{max}) and Mid-Day (Ψ_{min}) water potentials across species and sites (dry season)

Time of day	Species	Jonkershoek	Bainskloof	DuToitskloof
Pre-dawn	*Brabejum stellatifolium*	-0.27^{a} (0.02)	-0.66^{cde} (0.08)	-0.32^{a} (0.02)
	Metrosideros angustifolia	-0.36^{a} (0.06)	-1.10^{b} (0.11)	-0.43^{ae} (0.05)
	Acacia mearnsii	-0.52^{ad} (0.02)	-1.50^{f} (0.14)	-1.01^{b} (0.09)
Mid-day	*Brabejum stellatifolium*	-1.91^{a} (0.08)	-1.95^{a} (0.06)	-1.89^{a} (0.07)
	Metrosideros angustifolia	-2.65^{bd} (0.12)	-2.85^{de} (0.10)	-2.52^{b} (0.07)
	Acacia mearnsii	-2.60^{bd} (0.07)	-2.96^{ce} (0.07)	-2.65^{bd} (0.05)

All values are in MPa. Standard errors are given in parentheses. A factorial ANOVA was used to compare species and sites, with means separated using Fisher's LSD test. Within and between sites, means with *different superscripts* differ significantly ($P < 0.05$). $n = 5$

Table 5 $\delta^{13}C$ as indicator of water use efficiency (WUE)

Site	Species	$\delta^{13}C$ (‰)
Jonkershoek	*Brabejum stellatifolium*	-25.3^{a} (0.52)
	Metrosideros angustifolia	-23.6^{b} (0.41)
	Acacia mearnsii	-25.4^{a} (0.26)
Bainskloof	*Brabejum stellatifolium*	-24.8^{ad} (0.19)
	Metrosideros angustifolia	-22.7^{b} (0.59)
	Acacia mearnsii	-23.8^{bde} (0.32)
DuToitskloof	*Brabejum stellatifolium*	-26.8^{c} (0.46)
	Metrosideros angustifolia	-25.0^{ae} (0.48)
	Acacia mearnsii	-27.0^{c} (0.41)

A factorial ANOVA was used to determine species and site interactions. Within sites and species, WUE differ significantly ($P < 0.001$ respectively); there were no significant interactions between sites and species. Means were separated using Fisher's LSD test. Within and between sites, means with *different superscripts* differ significantly ($P < 0.05$). Standard error is given in parentheses

balances this against having high drought-tolerance because of its greater safety margin against cavitation. *B. stellatifolium* was as drought-tolerant as *A. mearnsii* in at least two sites, and experienced significantly higher minimum water potentials overall. This species also never reached water potentials low enough to reach its P_{50} level, and thus operated at a greater safety margin against runaway cavitation. Moreover, *B. stellatifolium* showed no significant difference in Ψ_{min} between sites. It is known that the major influence on Ψ_{min} measurements in plants is relative access to soil water (Ackerly 2004; Wikberg and Ögren 2004); one could thus deduce that *B. stellatifolium* has more effective access to groundwater in diverse environments, whereas other species do not. This species should persist in future drier conditions, and shows promise for use in post-clearing restoration.

In contrast, *M. angustifolia* functioned very close to, and often beyond its P_{50} threshold, showing the same trend as in a previous riparian study (Swift et al. 2008). The question is then—what other strategies might *M. angustifolia* use to tolerate or avoid drought, if any? It is possible *M. angustifolia* closes its stomata during low mid-day water potentials (not measured in this study), as was found for species that operate near

their hydraulic limit or P_{50} (Linton et al. 1998; Wikberg and Ögren 2004). Indirect evidence for this strategy was obtained from delta ^{13}C isotope ($\delta^{13}C$) results.

Delta^{13}C is seen as a biological expression of environmental conditions and provides an integrated measure to predict availability of water to plants (Stewart et al. 1995). Response to environmental conditions such as soil moisture is also species-specific (Ponton et al. 2001; Akhter et al. 2005). Akhter et al. (2005) showed that plants with a high WUE have the ability to maintain water uptake during drought by being hydraulically efficient through their conservative water use. This enables species to persist in a water-limited situation and is a form of drought adaptation. At two sites *M. angustifolia* exhibited significantly higher $\delta^{13}C$ values than the other study species, and therefore it adheres to a conservative water strategy. The indication is that although *M. angustifolia* functions close to its P_{50} value, and from this perspective appeared to be the least drought-tolerant of the natives, it might still persist in certain future drier conditions due to a different water use strategy, perhaps by closing its stomata (isohydry) for some time during the day. However, this may induce mortality through carbon starvation as reserves of carbon are exhausted under extended drought conditions (McDowell et al. 2008). Another strategy to achieve drought-tolerance within species is where xylem cavitation proceeds, but not through the whole plant (Rood et al. 2000). This is also known as hydraulic segmentation (Tyree et al. 1993), vulnerability segmentation (Tsuda and Tyree 2007) or branch sacrifice (Rood et al. 2000). Swift et al. (2008) suggested that species that operate near their hydraulic limit, such as *M. angustifolia* might employ branch sacrifice as an adaptation against drought conditions, as anecdotal field observations suggest. In contrast, *A. mearnsii* had low isotopic values, which confirms that it is a profligate user of water where it has access to large amounts, as suggested by Dye et al. (2001).

There is strong evidence that small changes in environmental conditions induce selection of improved plant adaptation strategies with regards to safe and efficient hydraulic transport (Ponton et al. 2001). A comparison of results over various stream-flow regimes yielded interesting data, which agree with the ecological strategies of the species described above. *B. stellatifolium* and *M. angustifolia* had their lowest P_{50} values at the intermediate flow site, Bainskloof, as opposed to the low flow site, Jonkershoek, suggesting that these species at Bainskloof are more drought-tolerant than at Jonkershoek. Jonkershoek and DuToitskloof, respectively the lowest and highest flow sites, also did not show apparent differences between species. Water potential (Ψ) data also suggested Bainskloof as the site where some species experienced significantly more stressed conditions. Additionally, Bainskloof was also the site where species had high WUE, again indicating it as a more drought-stressed environment, despite its intermediate stream flow regime. A similar result was found with *Vitis vinefera* where some sites were significantly more water-use efficient than others, promoted by a deficit in water availability (De Souza et al. 2005).

Our results thus challenge the hypothesis that species will be more drought-tolerant at lower stream-flow sites, as suggested by Swift et al. (2008) as well as other studies on riparian plants and their physiology (e.g. Willms et al. 1998; Rood et al. 2003). Riparian environments are typically highly heterogeneous in space (Naiman et al. 2005). Higher run-off does not necessarily ensure more plant water availability, and is therefore not an accurate predictor of in situ species drought-tolerance. Microsite or other factors such as site-specific geomorphology and microclimate (for example vapour pressure deficit) may play a more prominent role in selection towards greater drought-tolerance (Hupp and Osterkamp 1996). All three sites had highly permeable bed characteristics, though at Bainskloof the sample trees were found away from the water's edge, and grew in positions elevated above the stream, which may indicate less available groundwater, in contrast to the sample trees at Jonkershoek and at DuToitskloof. In addition, at Bainskloof the valley is more incised than the two other valleys, and the sampling sites are also located at higher altitudes (Mountain Stream Transitional as opposed to Foothills) (see Table 1) with lower potential for depositional processes, which may suggest lower groundwater reserves.

Conclusions

Vulnerability to cavitation is seen as the most important parameter in determining drought-tolerance in a tree (Cruiziat et al. 2002). Considerable variation

existed within and between species in their vulnerability to stem cavitation as measured by vulnerability curves, an indication of species-specific responses to withstand drought stress (different life-history strategies), and the variation within species under different environmental conditions (Cruiziat et al. 2002; Maherali et al. 2004). The invasive *A. mearnsii* was shown to be highly drought-tolerant, able to withstand low minimum water potentials and able to utilize more water, so it will be able to persist in future drier conditions, and must therefore remain a top priority for control. Fortunately, the co-occurring native, *B. stellatifolium* is also likely to persist under future drier conditions. It is well suited for restoration after clearing of invasions, which confirms results found by Swift et al. (2008), though the latter study was carried out over a much smaller geographic range. These consistent results between species and over sites strengthen the argument that this mechanistic approach to distinguish site-level drought-tolerance between plants and their drought-tolerance at a specific site, is a practical technique, with application in understanding future geographic distributions of species under climate change and their potential for use in restoration research. Vulnerability to cavitation and mid-day water potentials are also strongly linked for *A. mearnsii*, and therefore minimum water potentials are a valuable tool to predict its plant functional strategy with regards to drought (Bhaskar and Ackerly 2006). More research in understanding the mechanism of plant survival and mortality under different drought intensities and durations will be key in predicting species distribution and range for future drier conditions (McDowell et al. 2008). Lastly, streamflow *per se* is not robust enough to use as a screening tool when predicting drought-tolerance of species at a specific site as there was no relationship between drought-tolerance and river flows.

The management implications of this study are that sites could now be given top priority in clearing, e.g. DuToitskloof in this case, as this site has shown less drought-tolerance of both native species. We thus have another tool to assess the impact of uncontrolled invasion on native species in riparian zones, especially important when taking into consideration the projected rapid onset of drier conditions predicted for some regions (New 2002). However, specific micro-site conditions are also a major consideration in prioritising sites.

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